Leiocephalus aculeatus, sp. n.

Two lateral carinæ along the upper edge of the sides as well as the median dorsal one. Supraorbitals very broad, as in *L. iridescens*, Gthr.

Head as high as broad. Nostril posteriorly in an elongate nasal shield. Scales on the top of the muzzle numerous, polygonal, becoming larger towards the frontal region, where they pass into the two series of large interorbital plates, which are closely in contact. Three occipital plates—two rather large anterior, and one small posterior; two parietals on each side, the posterior one being very large. Orbital canthus sharp. A single series of very broad supraorbitals bordered with some small scales on each side. Only one elongate scale on the canthus between the upper angle of the orbit and the nostril, there being two such scales in *L. iridescens*. Upper labials four, narrow, elongate; a row of eight small scales above them; two rows of frenals, with an elongate infraocular scale. Ear-opening about half as large as the eye. The scales are everywhere keeled, sharp and dagger-like, with projecting points. A median dorsal crest of erect triangular scales extending on the tail; a weaker lateral one on each side of the back. Tail long, compressed, nearly thrice the length of the body.

Bronzed green, brownish on the sides, with vertical streaks. A white stripe from the ear to the fore limb, and another superiorly from the ear as far as the shoulder; another white stripe descending from the lateral carina to the fore limb.

	millim.
Distance of snout from eye	10
„ „ ear	23
„ „ fore limb	45
„ „ vent	100
Length of fore limb	50
„ third and fourth front toe	16
„ hind limb	85
„ fourth hind toe	25

Five specimens of the above described species were collected by Mr. Roff; they are from Moyobamba, Peru.

XXXIV.—*On the Homologies of the Cephalopoda.* By J. F. Blake, M.A., Lecturer on Comparative Anatomy at Charing-Cross Hospital.

There are two points of interest in the relations of the Cephalopoda which cannot yet be said to be settled. The first is their relation in homology, and thereby in their ontogeny, to the other classes of Mollusca; and the second, the relations of the Dibranchiate and Tetrabranchiate orders. These are questions on which our two great anatomists Professors Owen and Huxley have expressed decided opinions, which have not, however, been accepted by all, or perhaps the majority, of foreign naturalists. Constant accumulations also of new facts, especially in relation to the embryology of the Dibranchiates, force on us a reconsideration of the ideas derived solely from older ones, and even may lead us to put a different interpretation on the latter.

In order to compare the various classes of the Mollusca, we must place them in similar positions as defined by the first part of their alimentary canal and the circumœsophageal ganglia. The primitive form will then have a straight alimentary canal, with the cerebral ganglia above, the pedal more or less below, and the heart near the other end, its afferent vessels coming from the direction of the anus, and its efferent going towards the head. From this primitive form the rest may be deduced by a bending forwards of the anal end, carrying with it the heart and its branchiæ. On the direction of this flexure of the intestine great stress has been laid by Huxley; but I have not found much notice taken of it by foreign writers. It is obvious that such a flexure *may* take place in two opposite directions; and these have been defined by Huxley, in his recent work on the Anatomy of the Invertebrated Animals, as follows:—In the first the cerebral ganglia lie within the general angle formed by the intestine; in the second it is the pedal ganglia which lie within it. Unfortunately these two directions have been called respectively the "hæmal" and "neural." Of course the flexure must in every case be neural, as tending to bring the anus nearer to the nervous centres; and it must generally be also hæmal, for the heart usually accompanies it in its changes. In particular the Cephalopoda are said to have a neural flexure. In these the intestine is bent to the side of the pedal ganglia; but yet its direction is towards the heart, which lies on the underside. In the Pulmonata the intestine bends to the side of the cerebral ganglia; and yet its direction is towards the heart, which lies on the upperside. These latter were formerly said to have a neural flexure; but it is now called hæmal*. Taking this last view, and substituting the terms "cerebral" and "pedal" for hæmal and neural, the distinction between the classes is most marked, the Pteropoda

* Huxley, 'Morphology of Ceph. Mollusca,' 1853, and 'Introduction to Classific.' p. 39, with 'Manual of Invert. Animals,' p. 514.

alone agreeing with Cephalopoda in having a pedal flexure, that of all the rest, except Nudibranchs and Tectibranchs (which have scarcely any flexure at all), being cerebral. A point of difficulty still remains respecting this. Although the heart always accompanies the intestine in its flexures, and its afferent vessels come from the direction of the anus, yet when the intestine is rectified it appears to have a different relation to it. When the intestine is naturally straight, as in the Nudibranchs &c., the heart lies on the cephalic side—I believe, without exception. It would have the same position in the Cephalopoda and Pteropoda. But in the Heteropoda (*Atlanta*) certainly, in the Pulmonata, and, I think, also in the Pectinibranchs it would lie on the *pedal* side. It is not easy to say whether the heart lies within or without the curve formed by the intestine (on which its position, when the latter is rectified, would depend) when, in point of fact, it lies at the *side*. Perhaps, however, it is all a matter of accelerated growth. In the Lamellibranchs the intestine pierces the heart, which therefore lies on both sides of it; and the branchiæ surround the anus in *Doris* &c. Both tend to develop most on the outside, while the portion lying within the body aborts. According, therefore, as the flexure is cerebral or pedal does one or the other part of the circle become persistent, under the condition of being exterior. But the original flexure itself may have been caused by the increased growth of that side which now lies outside. This does not, certainly, account for the one-sided hearts of the Nudibranchs; but it *does* account for the different direction in which the shell of a cephalopod and of a snail is coiled: the former has its convexity, and therefore its greatest growth, on the pedal, the latter on the cerebral side. In both cases the convex side of the shell is on the side of the heart. In the case of the *Spirula*, not only the convex side of the shell, but the whole last chamber of the shell lies on the side of the heart.

We should conclude from the above observations that the Cephalopoda branched off from the main molluscan stem, through the Pteropods, at an earlier period than the development of ordinary Gastropods; and, indeed, we find their remains in deposits of earlier date than those containing the latter.

The next point of importance is the homology of the foot and other non-pallial outgrowths, on which, in fact, depends the position in which we should suppose the animal placed for comparison. In Prof. Huxley's paper on the Morphology of the Cephalous Mollusca (Phil. Trans. 1853), the line along the base of the foot is taken to have a constant direction, and, the arms of the cephalopod being taken as homologous to the foot, the intestine is made to begin in a vertical direction, while in all other mollusks (except Pteropods) it is made to commence in, and have generally, a horizontal direction. It would seem, to say the least, more natural that the position of the intestine and the nervous centres should be constant, rather than that the whole animal should be displaced for the sake of the, *ex hypothese*, greatly modified foot. Prof. Owen, in a recent paper, calling the side on which the cerebral ganglia are placed in Cephalopods dorsal, and the opposite side ventral, states that this is assented to by every malacologist. It may be wrong for all that: the foot *may* be always horizontal; the animal *may* grow vertically instead of horizontally; but what is the proof? Prof. Huxley states it as follows:—"Whether we have to do with a cephalopod or with an ordinary mollusk, the first step in the development is the separation of the blastoderm into a central elevation, the mantle, and certain lateral portions. Now these portions become in the Gastropoda the head and foot; in the Cephalopoda the head and arms. It follows, therefore, that the arms of a cephalopod are homologous with the foot of a gastropod."

Now, at the earliest stage at which such organs are recognizable, we have, for example, in *Paludina vivipara* (Leydig, Zeitsch. für wiss. Zool. ii. 1850, p. 127, &c.) the alimentary canal in a straight line, a median outgrowth on one side (the foot), and on the other a raised ciliated circle (the velum); subsequently the growth of the shell and mantle near the anal end, but slightly on the foot side, displaces the anus forward by taking its place at the end of the intestinal axis. Subsequently the foot grows out behind and before, so that its main axis becomes parallel to the alimentary canal. If now we place the mantle at the top and the mouth at the bottom, we may call the velum and tentacles on one side, and the foot on the other, lateral outgrowths; but the alimentary canal will run, as in a cephalopod, straight into the mantle-cavity, which direction remains (as far as the stomach) unchanged during development, while the foot *does* change its position by its fore and hind outgrowths. In the development of the Cephalopoda the partial segmentation of the ovum and the possession of a large yelk or nutritive vitellus displace the mouth, which should arise on the underside of the mantle elevation, and causes it to appear near the circumference of the blastoderm, the anus appearing later at the opposite end of the diameter; *but there is never a straight canal between them*; their cavities both grow into the hollow of the mantle-cavity, and meet near its base. Thus the first portion of the alimentary canal, *as soon as it is formed*, has the same direction with respect to the mantle as in the Gastropods. The direction, therefore, that is normal is this one, namely direct into the mantle-cavity, and not parallel to the edges, as Huxley's diagram would make it; and we must place the Cephalopod for comparison with the Gastropod with the œsophagus in the same direction, either both horizontal or both vertical. As the line parallel to this on the cerebral side of the latter is called dorsal, and the basis of the foot ventral, so in the former the *os sepiæ* lies on the dorsal surface and the funnel along the ventral, while the shell of the *Nautilus* comes "behind."

And now as to the foot. There is this essential difference between the foot of a Gastropod and the arms of a Cephalopod, strongly insisted on by Grenacher (Zeitsch. für wiss. Zool. vol. xxiv., 1874), that the foot is an unpaired organ, being situated in the median line. It shows a tendency to spread forward and backward, but not laterally; and where it is divided the several parts succeed each other in a longitudinal direction. This character is seen even in Lamellibranchs which have a paired shell. Only the anterior portion in any mollusk shows itself slightly bilobed. The arms of the Cephalopod, an animal with a *single* shell, are, on the contrary, from their very commencement, paired; and they are thus lateral in a very different sense from that in which the foot is so. This is to me, as it is to Grenacher, conclusive against their homology. The one can only be compared (with Huxley) to the dorsal fin of a fish; the others with its paired fins. But we must seek light also on this question from the relations of the nerve-ganglia. On this point, too, there seems to be a conflict of opinion; but the testimony appears to me conclusive against the homology I am disputing. In the first place, it might be said, the pedal ganglia are paired, therefore the foot itself is in its nature paired; yet the buccal ganglia and some of the visceral ganglia are often paired; and no one will assert the alimentary canal to be any thing but a single organ. In the next place, the normal arrangement of nerves in a Gastropod consists of two cerebral ganglia above the œsophagus and two pedal ganglia below, with which may be more or less united a pair of splanchnic ganglia behind. The auditory organs are in connexion with the pedal ganglia when not directly supplied from the cerebral. There is thus but one nervous ring. Now in the *Nautilus** the ring is subdivided, and there are *two* sets

* Owen, 'Memoir on the Pearly Nautilus,' 1832; Macdonald, Phil. Trans. 1855.

of far-separated subœsophageal ganglia. The auditory organ arises at the junction of the upper and lower ganglia, but more in relation to the hinder than the front band of the latter. The hinder pair have been called the splanchnic, and the front pair the pedal; but their position in this case would be anomalous, and it is the hinder ganglia which chiefly supply the shell-muscles, which, though not homologous, are to a certain extent analogous to the foot. But if the *Nautilus* leaves us in doubt, a *Sepia**, an *Ommastrephes*†, or an *Argonaut*‡ is clear. In these there are *three* pairs of subœsophageal ganglia. The front pair supply the arms, the *middle* pair supply the funnel and the auditory organs, the hinder pair supply the viscera. If, then, we are to take any *independent* guidance from the nerves, the front pair are *not* pedal, but belong in all the Cephalopoda to organs not developed in the adult Gastropoda; the middle pair correspond to those in the latter class called pedal; and the hinder pair are the splanchnic.

To what, then, are the arms homologous? Lovén, in 1848 ('Bidrag till Kännedomen om utwecklingen af Moll. Acephala') called them a persistent velum; and to this view Grenacher gives his adhesion. There seems, however, at first sight a fundamental objection to this, as Grenacher himself points out. The velum is always developed on what will be the cerebral side of the œsophagus, while the arms of the Cephalopod arise at first on the *opposite* side, or where the *foot* should be. It is no answer to this to say, without proof, that as they are not needed for nutrition they may shift their place, or, because the œsophagus is unpaired, to make light of its relative position. Such a treatment of questions would render homology hopeless. It seems to me the true solution will be found by asking, What is the velum of a Gastropod? Huxley first, then Gegenbaur, and lastly Ray Lankester have shown how these ciliated bands may be traced from one class to another—sometimes in the larva only, and sometimes as an adult organ (see Lankester on Embryology and Classification, 1877). In the primitive condition they formed a circle round the œsophagus, and as often as not are thrown out into long processes; with a change in the direction of the intestine their uniformity is broken, and part dies away, while the other part is left, forming a circle surrounding, not the œsophagus, but a portion of the body on one side of it, the foot being on the other. Since then, in the Gastropoda, the intestine

* See Huxley, Anat. of Invertebrates, p. 526; after Garner, Trans. Linn. Soc. 1836.

† Hancock, Ann. & Mag. Nat. Hist. 1852.

‡ Beneden, Mem. Acad. Brussels, vol. xi. 1838.

turns to the cerebral side, we have the "velum" formed on that side, whereas in the Cephalopoda, the flexure being to the opposite side, we have what we may call the "antivelum" on the pedal side. Thus the arms are homologous to the opposite portion of the architroch to that which forms a velum, and merely afford another instance in which these primitive formations are retained as functional organs. Moreover, from within the circle of the embryonic velum rise up in some Gastropods two long retractile tentacles; in like manner from within the later-formed circle of the antivelum rise up the two retractile tentacles of the Decapods.

If such be the true homology of the arms, what in the Cephalopoda represents the foot of other Mollusca? When we remember that even among the Lamellibranchs the foot is sometimes wanting, that it is very variously developed in the Gastropoda, and has merely a rudimentary representative in most of the Pteropoda, we cannot make sure of its being present at all. That it should be represented by the two halves of the funnel, as Gegenbaur supposes, is as objectionable an idea as its homology with the arms, and for the same reason—though, being more closely connected with the region of the foot, they may be supplied from the pedal ganglia. I can only suggest one median unpaired outgrowth which *may* represent it; and that is the valve within the funnel, which occurs in a great number, and especially in the *Nautilus*, which is least removed from the general type. This, however, must be doubtful, as the development of this valve has not been observed.

The recognition of the two funnel-halves of the adult *Nautilus* and the embryonic Dibranchiate as part of a second outgrowth surrounding the body, to which the name of epipodium has been given by Huxley, is pretty general; and there seems to be nothing against it. Grenacher has shown that each half is originally again in two parts, one following the other longitudinally; and one of these parts only he reckons homologous to the sails of the Pteropods.

With regard to the relations of the *Nautilus* to other Cephalopoda, it is remarkable how every additional fact in the development of the latter shows the former to represent embryonic stages; and this is the more interesting as the allies of the *Nautilus* certainly preceded the Dibranchiates in their appearance on the globe. The following points, old and new, are most noticeable in this respect. In the *Nautilus* and in the embryo Dibranchiate the funnel is in two halves, but unites into a single tube in the adult of the latter. In the *Nautilus* and embryo Dibranchiate up to a late stage there is no ink-bag, which only comes in the third period of the development of the latter; and, moreover, the *Spirula*, which is most nearly allied to the *Nautilus* by its siphonated shell, has the smallest ink-bag. Again, the *Nautilus* has its eye a simple cavity, opening externally by a minute aperture; and this is one stage of the development of the eye of a Dibranchiate. In the *Nautilus* the auditory organs are found close beneath the eyes; in the Dibranchiates they are at first found in the same position, and only gradually grow closer and closer together till they come into contact with each other on the ventral side. Finally the tentacular and labial processes of the *Nautilus* are flattened more or less, and lie one within the other. In the development of the Dibranchiate the arms rise as broad flat processes also, and one pair lies within the rest.

This last point throws light upon another question which I wish to discuss—namely, whether the six or eight processes on which the tentacles of the *Nautilus* are found are homologous to the eight arms of the *Octopus*, each tentacle representing a sucker, or whether each tentacle is homologous to a whole arm of an *Octopus*, the number having been greatly reduced. The former view was propounded by Valenciennes *, but has been contested by Owen †. Though to my mind highly interesting and suggestive, it has scarcely been noticed by other writers. Prof. Owen brings forward four reasons against this homology. First, that the general order of development is from the multiple to the simple, and therefore we ought to expect more arms in the *Nautilus*. In order that this might be true of the Cephalopod's arms we ought to find in the development of the Dibranchiates that they arose in greater numbers, and ultimately grew together into the eight. But Grenacher has now shown that first three arms arise as simple broad expansions on each side, and at a later period the suckers and the other arms appear, the fourth pair being but a process of the third, while of the first three the earlier ones lie partially within the later, and the third is the largest; so that, if we accept the above homology, the *Nautilus* exactly represents an early stage in this as well as in other respects; for it also has the fourth or anterior pair but feebly developed, being represented by but one tentacle beneath the hood. The third pair are the largest, and the other two are surrounded by it. Thus development in this case is not from the multiple to the simple in Prof. Owen's sense. It is, however, so in another sense, and in one which makes for this homology.

* Annales du Musée, 1841.

† Ann. & Mag. Nat. Hist. 1843, vol. xii.

The second objection is, that the nerves of the tentacles arise independently from the ganglia, and each one is therefore homologous to a single arm, the rest having aborted. But as each sucker of the Argonaut, as shown by Beneden*, has its ganglion and nerve, it is these that are homologous with the several tentacles of *Nautilus*, which each have a single nerve arising from a ganglion, not yet separated at the base—the only difference being that each tentacle is separate, and the development being from the multiple to the simple, the suckers on the Dibranchiates are collected onto an arm whose nerve though gangliated is single. The other two objections need not be noticed, as they have been answered by implication; but there is an argument in favour of this homology derived from knowledge acquired since the time of that paper. One of the most remarkable features of the Dibranchiates is the hectocotylization of one of the arms of the male, whereby it is made an organ subservient to reproduction, though there is no constancy with respect to the particular arm which undergoes this change. Now Van der Hoeven† has shown, and Keferstein‡ has confirmed the fact, that the male *Nautilus* in like manner suffers hectocotylization, by which the organ called the spadix is produced, an organ which, like that of the Argonaut and others, has a glandular function, and is brought into relation with the spermatophores. Now if each tentacle were homologous to an arm it should be one of the tentacles, or part of one, which is so modified. But what is the case? In the female the corresponding labial process is divided into two parts, one supporting four tentacles and the other eight; and it is the corresponding *four* tentacles in the male which make up the spadix within which they may be seen in transverse section. Thus it is part of one of the processes whose tentacles are modified in the *Nautilus*, just as it is one of the arms whose suckers are modified in the Octopod; *ergo* the process is the homologue of the arm.

Again, there is a word to say about the *hood* of the *Nautilus*. On account of there being a tentacle contained in a cavity on each side within, this has been taken to represent the two foremost tentacular processes, or, as I may now call them, arms of great substance, and which have grown together; and so the eight are made out. Whether this is the right way to look at them, or whether the hood is not an independent organ which has grown to the single-tentacled arms lying immedi-

* "Mémoire sur l'Argonaute," Acad. Brussels, vol. xi. 1838.

† Wis. en Natuurk. Verh. der Koninkl. Akad. deel iii. 1856; and Ann. & Mag. Nat. Hist. 1856.

‡ Bronn's 'Klassen und Ordnungen,' Band iii. 1865.

ately beneath them, is rather difficult to say, and is one point which would be settled by a knowledge of the *Nautilus*'s development. On the one hand, as was originally suggested by Van der Hoeven, and has been expounded recently by Owen*, the hood in the extinct allies of the *Nautilus* had the power of secreting calcareous or horny matter known as the *aptychus*; and this leads us to the shell of the Argonaut, secreted by the anterior pair of arms, which would thus be homologous with the aptychus if the hood were a modified pair of arms. On the other hand, if we carefully examine the upper surface of a *Sepia* and other Decapods in front of the calcareous "bone" and just behind the eyes, we shall find two hardened plates (called neck-plates by Keferstein), whose shape and ornaments are so similar to those of the aptychus as to make us almost certain of their homology; and these, therefore, must represent the hood of *Nautilus*, with whose position they agree. Yet we do not know that these two plates are in any way connected with the arms, either in the adult or during development; but they seem to belong to the anterior part of the epipodial ring. Either homology is so interesting that one would wish to find some way of adopting them both.

Finally, is the bone of the *Sepia* homologous with the shell of the *Nautilus*? Not exactly, I think. The homologues of the latter may be seen in the shell of the *Spirula* and the phragmocone of a Belemnite; but any representative in the *Sepia* must be sought in its mucro, and not in the mass of the bone. This opinion (for at present it is little more than an opinion) seems to gain weight by a consideration of the fossil genus *Ascoceras*. This occurs in the Upper Silurian strata, a very probable date for the near approach of the Dibranchiates. In it we find two sets of septa : the one set are at the base of the shell of the ordinary kind pierced by a siphuncle; the other set are in the body-chamber. They lie on one side obliquely; they run into one another in their curves; and they are penetrated by no siphuncle. In other words, the shell presents us with the characters of the *Nautilus*-shell at its base, and with those of the *Sepia*-bone above; and from it we may perhaps perceive the true relations of these two structures. Further details on this genus cannot now be entered upon; but they will be given in my forthcoming 'Monograph of the Fossil Cephalopoda of Great Britain.'

Proc. Zool. Soc., Jan. 1879.